

Plant growth and survival of five introduced and two native/naturalized perennial grass genotypes exposed to two defoliation managements in arid Argentina

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Abstract

The field performance of the native *Pappophorum vaginatum*, the naturalized *Eragrostis curvula* and various cultivars of the introduced *Achnatherum hymenoides* and *Leymus cinereus* was evaluated as potential forage resources in rangelands of arid Argentina during the warm seasons of 2007/2008 and 2008/2009. Plants of these grass species, obtained from seeds, were transplanted to the field in 2006, when they were 1 year old. During the study years, there were two defoliation managements: plants of all study genotypes either remained undefoliated (controls) or were defoliated twice a year during spring at 5 cm stubble height. Despite tiller number being lower ($P < 0.05$) on defoliated than on undefoliated plants, and total leaf length per unit basal area being similar ($P > 0.05$) between defoliation managements by mid-spring, there were no differences ($P > 0.05$) in dry weight production between defoliated and undefoliated plants in all genotypes at the end of the second growing season. Plants of one or more of the introduced genotypes showed a similar ($P > 0.05$) or greater ($P < 0.05$), but not lower, tiller number per plant and per square centimetre, daughter tiller production, total leaf length

and dry weight production per unit basal area than the native species at the end of the first and/or second growing seasons. These morphological variables were similar ($P > 0.05$) or greater ($P < 0.05$) in the native than in the naturalized genotype. Plant survival, however, was lower ($P < 0.05$, overall mean = 20%) in the introduced than in the native (>70%) or naturalized (>39%) genotypes at the end of the first or second growing seasons.

Keywords: *Achnatherum hymenoides*, *Eragrostis curvula*, *Leymus cinereus*, *Pappophorum vaginatum*, plant demography, plant growth

Introduction

The cattle production industry in 75% of continental Argentina, characterized by arid and semi-arid areas, is based upon grazing of native vegetation (Fernández and Busso, 1999). Unfortunately, most of these areas have been exposed to grazing and fire mismanagement, resulting in shrub encroachment and the local disappearance of acceptable perennial forage grasses for cattle grazing (Fernández and Busso, 1999). As a result, rangelands of central Argentina have few warm-season, native perennial grasses that are acceptable forages to grazing livestock (i.e. *Pappophorum vaginatum*; Busso *et al.*, 2004). Therefore, there is an imperative need to increase perennial grass species in this region (Anderson, 1980) to address the increasing cattle production and need for additional forage. Severe water stress, especially during the warm

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season, is another constraint the vegetation might eventually be exposed to (Giorgetti *et al.*, 1997). The need to develop more appropriate forage resources for semi-arid grasslands and rangelands was emphasized by various researchers worldwide (Torres, 2010).

Various C₃ perennial grass genotypes were worthy of consideration to complement use of the native/naturalized genotypes in our region. Those genotypes, coming from the western arid and semi-arid USA rangelands, included (i) *Leymus cinereus* cvs 'Magnar' and 'Trailhead' and (ii) *Achnatherum hymenoides* (Romer & J.A. Schultes) Barkworth cvs. 'Paloma', 'Nezpar' and 'Rimrock'. These genotypes grew during the warm, but not the cool, season in our region. An additional, warm-season, perennial grass tested in the region was *Eragrostis curvula* cv. 'Tanganyika'.

Results on productive performance and plant survival in native versus introduced species are scarce (Wilsey and Polley, 2006) and contradictory (Vilá and Weiner, 2004). There are examples where the introduced species have responded very flexibly and optimally to the colonized environment, either growing more vigorously or distributing more resources to reproduction (Maron *et al.*, 2004). However, it needs to be considered that native species of any given environment are adapted to the local conditions of such environment. Therefore, greater plant establishment and persistence should often be expected for native than for introduced species. Insufficient water availability has, in the past, been the main cause of failures in the attempts of introducing plant species in arid rangelands (Bleak *et al.*, 1966). These authors emphasized that appropriate management of native vegetation would be the best approach to achieve a good plant cover of forage that is acceptable to grazing livestock in those rangelands.

There are several examples, however, where introduced species have contributed to increased forage supply in cultivated and rangeland areas of Argentina and other countries: (i) *Agropyron desertorum* (Fischer ex Link) Shultes from Eurasia into the Western US rangelands; (ii) *Eragrostis curvula* (Schrader) Nees and *Tetrachne dregei* Nees, from South Africa into the cultivated area of the semi-arid Pampas region, and into the central rangelands of La Pampa Province, Argentina respectively; and (iii) *Cenchrus ciliaris* L. from Africa into the Catamarca Province, Argentina (Fernández *et al.*, 1991; Briske and Richards, 1995; Ruiz and Terenti, 2012). Among the reasons for these successes are (i) a greater competitive ability than the native forage grasses and (ii) a high plasticity to various habitat conditions (i.e. extreme pHs, water stress, soil types; Fernández *et al.*, 1991; Briske and Richards, 1995; Ruiz and Terenti, 2012). Therefore, we can expect that traits related with high competitive ability

to various habitat conditions might be useful characteristics that could make plant introductions successful.

Several studies have been made on the morphophysiology, demography, plant growth and responses to grazing in *P. vaginatum*, *L. cinereus*, *A. hymenoides* and *E. curvula* (Fernández *et al.*, 1991; Ogle *et al.*, 2002; Torres *et al.*, 2011). Although there are many studies, it is not clear yet which are the mechanisms responsible for grazing tolerance in these species. In addition, performance of the introduced genotypes might be different in Argentina than in other locations where previous work has been done. This is because climate and soil physico-chemical characteristics influence species introductions into degraded areas (De Graaf *et al.*, 1998).

Tolerance to defoliation is given by the speed of photosynthetic surface reestablishment after such disturbance is produced (Briske and Richards, 1995). Rapid daughter-tiller production is a major factor contributing to defoliation tolerance (Briske and Richards, 1995). Timing of defoliation has direct effects on subsequent shoot growth rates, and plant dry-matter production and survival (Briske and Richards, 1995). Greater total leaf lengths have been produced after active meristems remain on the plant after defoliation (Becker *et al.*, 1997). Therefore, we hypothesize that a greater daughter-tiller production in the native and naturalized than in the introduced grasses determine a greater dry-matter production in *P. vaginatum* and *E. curvula* than in the other introduced genotypes.

Objectives of this work were to compare productivity, survival and some morphological traits that might contribute to determine grazing tolerance of seven perennial grass genotypes (one native, one naturalized and five introduced) under two defoliation managements (undefoliated controls versus early and mid-season defoliations) during each study growing cycle. These objectives would contribute to develop a better understanding of grass growth response to aid management.

Materials and methods

Study site

We conducted one study spanning 2 years (2007/2008 and 2008/2009), involving genotype and defoliation treatments, and multiple measurements. Studies were performed in the Chacra Experimental de Patagones, Buenos Aires, Argentina (40°39'S; 62°53' W; 40 m.a.s.l.), within the Phytogeographical Province of the Monte (Cabrera, 1976).

Climate is temperate arid to semi-arid, with higher precipitations during the spring and autumn seasons

(Giorgetti *et al.*, 2000). Long-term (1981–2009) annual rainfall is 412.9 ± 159 mm (mean \pm 1 SD), with a mean annual temperature of 14.6°C , absolute minimum temperature of -7.6°C (August), absolute maximum temperature of 43°C (January), mean annual relative humidity of 60%, and mean annual wind speed of 13 km h^{-1} . Mean rainfall values from September to May (the warm-season growing period) were 178 and 135 mm during 2007/2008 and 2008/2009 respectively. These values were lower than the long-term average (1981–2010; 336 mm) during that growing period. Within the region, fertilization and irrigation are not an option: 55% of the years within the long-term mean (1981–2009: 412.9 mm; range = 195.5–877.3 mm) have shown an annual precipitation equal to or lower than 390 mm. High variability in annual precipitation is typical of arid environments (Noy-meir, 1973). Climate conditions were registered by a meteorological station located at the study site and are depicted in Figure 1.

Soil is a typical Haplocalcid. Average pH is 7, and depth is not a constraint in the soil profile. The plant community at the 'Monte' study region is characterized by an open, shrubby stratum which includes different quality, herbaceous species for cattle production (Giorgetti *et al.*, 1997). Dominance of a particular grass or shrubby species in the study region is partially dependent on grazing history and fire frequency and intensity (Distel *et al.*, 1996). A description of the study species is provided in Table 1.

Experimental design and defoliation managements

Plants used in this study were obtained from seeds in the laboratory during spring 2005. Pre-germinated seeds were put on plastic pots (10 cm diameter and 15 cm height) which remained under natural, rainfed conditions until transplanting time in 2006. Thereafter, this study was conducted on a natural grassland excluded from grazing; one enclosure (30×40 m) to domestic livestock was established on this grassland. The natural vegetation within the enclosure was taken out from the soil by hand, trying to make the least amount of soil disturbance. The soil had not been cropped during at least the last 30 years. The experiment was initiated on November 2006, by establishing 98 single-genotype plots from 1-year-old transplant [7 genotypes (*P. vaginatum*; *L. cinereus* cvs. 'Magnar' and 'Trailhead'; *A. hymenoides* cvs. 'Paloma', 'Nezpar' and 'Rimrock'; *E. curvula* cv. Tanganyika) \times 2 defoliation managements (unclipped controls or plots clipped twice during the growing period) \times 7 replicate]. A completely randomized design was used during plot establishment. Each plot constituted an

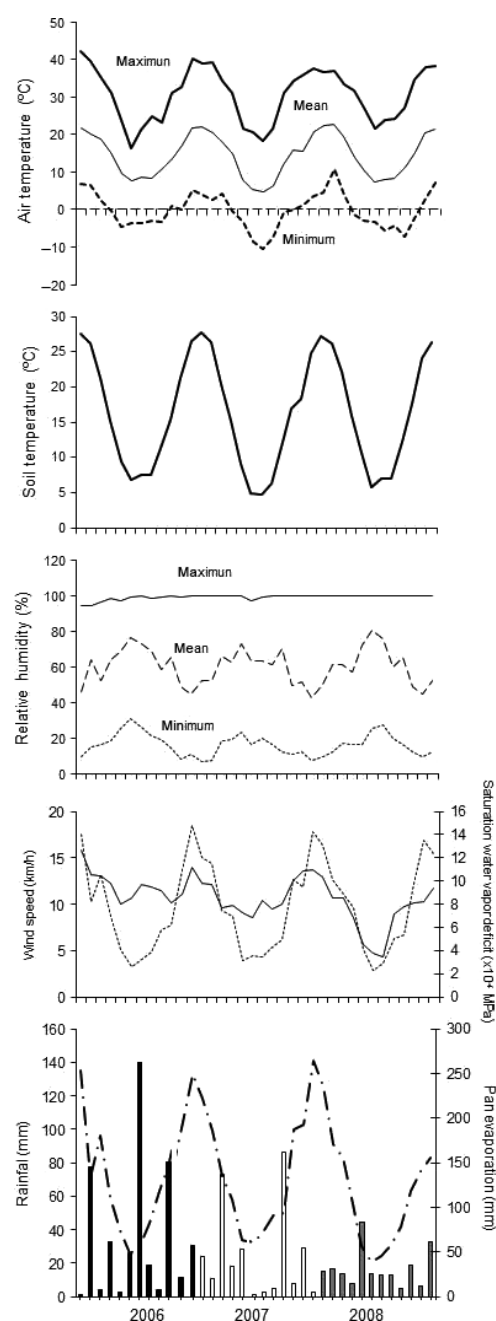


Figure 1 Absolute monthly maximum and minimum, and mean monthly air temperatures; mean monthly soil temperatures at 0–20 cm soil depth; absolute monthly maximum and minimum, and mean monthly relative humidities, mean monthly wind speed and saturation water vapour deficit, and mean monthly pan evaporation and monthly rainfall during 2006, 2007 and 2008 at a meteorological station located at the study site. Annual precipitations during 2006, 2007 and 2008 were 428.1; 287.5 and 198.0 mm respectively.

Table 1 Some major characteristics of the perennial grass genotypes used in this study

Genotype	Origin	Description	Reference
<i>Pappophorum vaginatum</i>	North and Central, up to northern Patagonia, Argentina	Warm-season, C ₄ native bunchgrass acceptable to grazing livestock Mean biomass production (1984–1992) = 560.9 ± 130.8 kg ha ⁻¹ year ⁻¹ (mean ± 1 SE); reduced by overgrazing Tolerant to frost while dormant High seed production Seeds cannot be seeded by conventional drilling because of disseminule morphology (hairy anthesis + long awn)	Cano (1988), Giorgetti <i>et al.</i> (1997), Allen <i>et al.</i> (2011)
<i>Leymus cinereus</i> cv. 'Magnar'	Saskatchewan, Canada	Very drought tolerant, long-lived and productive. It withstands flooding Cool-season, C ₃ , rhizomatous genotype acceptable to grazing livestock Excellent for enhancing soil structure Seeds can be seeded by conventional drilling	Majerus (1992), Johnson <i>et al.</i> (2003), Allen <i>et al.</i> (2011)
<i>Leymus cinereus</i> cv. 'Trailhead'	Roundup, MT, USA	Same as 'Magnar', but also it can survive in areas with 150 mm annual precipitation	Majerus (1992), Johnson <i>et al.</i> (2003), Chambers and Miller (2004), Allen <i>et al.</i> (2011)
<i>Achanatherum hymenoides</i> cv. 'Paloma', 'Nezpar' and 'Rimrock'	'Paloma': Pueblo, CO, USA 'Nezpar': Whitebird, ID, USA 'Rimrock': Billings, MO, USA	Excellent for rangeland improvement and land reclamation Densely tufted, very drought tolerant, nutritious C ₃ bunchgrasses acceptable to grazing livestock Seeds can be seeded by conventional drilling	Jones (1990), Allen <i>et al.</i> (2011)
<i>Eragrostis curvula</i> cv. 'Tanganyika'	South Africa	Warm-season, C ₄ naturalized bunchgrass acceptable to grazing livestock Biomass production without fertilization of a seeded forage crop was between 4000 and 5000 kg ha ⁻¹ year ⁻¹ depending on vegetation management (without or with autumn resting from livestock grazing respectively) Tolerant to frost while dormant Drought tolerant Its establishment and subsequent performance is limited to a series of successive wet years Seeds can be seeded by conventional drilling	Fernández <i>et al.</i> (1991)

experimental unit. Defoliation managements were applied at random within each set of single-genotype plots. Plants on these plots were irrigated during spring 2006 and allowed to establish during a year

previous to the study initiation in 2007/2008 and 2008/2009. We used vigorous transplants, instead of obtaining plants directly from sowing at the field, to improve the likelihood of successful plant establish-

ment. Within each plot, plant distance among plants in horizontal and vertical lines was 30 cm (from centre to centre on each plant crown; $3 \times 4 = 12$ plants). In this way, competitive relationships among plants were most likely similar. Similar approaches for transplant disposition within plots have been reported in other studies (Flemmer *et al.*, 2002). During the study, plants were exposed to natural rainfall.

The first defoliation (i.e. clipping) was made using scissors during winter (the plant dormancy period) across all plants (i.e. across all plots) of the seven genotypes to remove aftermath in 2007. The purpose was that only aerial plant growth produced above 5 cm stubble during the subsequent warm growing season was used for sampling. This defoliation did not count as a treatment because plants were dormant at this time (i.e. aerial tissues were dead at this removal time, and thus it was not the commencement of the defoliation managements). Defoliating plants while they are in a dormant stage, with minimal physiological function, does not influence future plant performance (Schacht *et al.*, 1998). Thereafter, plants in half of the plots were defoliated twice within each of the study growing cycles (i.e. the defoliation treatment was repeated for all plants on both dates in each growing cycle). During 2007/2008, defoliations were made on 5 and 11 November (mid-spring) 2007, and during 2008/2009, they were done on 19 November and 20 December 2008 (late spring). In the other half of the plots, the control plants were defoliated in winter 2007 and 2008 (i.e. during the dormancy developmental morphology stage) and in autumn 2008 and 2009 respectively, so their biomass was the forage accumulated during each growing season. Defoliation treatments were delayed in the second growing cycle because of a lower rainfall during September to December in 2008/2009 (see Figure 1: 62 mm; i.e. a smaller plant growth) than in 2007/2008 (125.5 mm). This defoliation management mimics the short duration – high intensity, rotational-stocking system applied at the 'Monte' vegetation in the Chacra Experimental of Patagones (see Giorgetti *et al.*, 2006 for details; mean = 29.2 animal unit ha^{-1}). Within this system, some acceptable forage can be grazed twice by grazing livestock during their at least 30-day stay in the paddocks (Giorgetti, 1995). In Argentina, an animal unit is defined as the annual average dry forage requirement of a 400-kg cow that goes through gestation and subsequent nursing of a calf, until the 160-kg, 6-month-old calf is weaned, including the forage consumed by the calf (Giorgetti *et al.*, 2006). Defoliations were applied to the same plants in each year. In all cases, plants were defoliated leaving 5 cm stubble height. Defoliations were made during the vegetative stage and immediately after differentiation of the

growth apex from vegetative to reproductive. It means that actively growing meristems (intercalary and leaf primordia in the growth apex) remained on the plants after the defoliation events.

We have to acknowledge that no plants that remained undefoliated throughout the entire study. Information on defoliation treatments and their purpose is summarized in Table 2.

Measurements

A summary of measurements made, measurements dates and why they were taken is provided in Table 3. A more detailed description follows:

Height of the apical meristem

Tillers of all seven genotypes were dissected every 2 weeks (Table 3) and observed under a binocular microscope to determine both the developmental stage and height of the apical meristem.

Components of leaf-area production

Tiller growth and demography were periodically determined. Ninety-eight randomly chosen plants were marked for this purpose (one per plot) in 2007/2008; we used 70 plants during 2008/2009 because *A. hymenoides* cvs. 'Nezpar' and 'Rimrock' were unable to persist after the drought years and defoliation managements. On each one of these plants, one current-season tiller was permanently marked with wire cables. Plant circumference of green basal areas (used to calculate total green basal area), number of total tillers and number of daughter tillers produced by each marked tiller were determined on each plant. Total tiller number per plant was divided by total green basal area to obtain tiller number per square centimetre. In addition, total leaf length [blades + sheaths (green + dry)] was measured on each marked tiller. These measurements followed those of Busso *et al.* (2003). Total leaf length data were used to calculate growth rates following Larcher (2003). The timing for the measurement of each variable is indicated in Table 3.

Aboveground biomass production

Aboveground biomass was harvested using scissors at the time of defoliation (springs 2007 and 2008) on defoliated plants, and at the end of the growing seasons (autumns 2008 and 2009) in all study plants. This allowed us to obtain the total aboveground biomass productions of defoliated plants and undefoliated controls during 2007/2008 and 2008/2009. All

Table 2 Summary of applied treatments, treatment dates and purposes. Plant used during the second growing cycle (2008/2009) received the same treatments than those on the first growing cycle (2007/2008)

Treatment	Date of treatment (season; plant developmental morphology stage)	Purpose of treatment
Removal of aftermath at 5 cm stubble height on all study plant (this was not the commencement of the defoliation treatments)	1 August 2007 (mid-winter; dormancy)	To determine aerial plant growth produced above 5 cm stubble during the following warm growing season, and various traits related to plant growth (see Table 3), as affected by two defoliation managements (clipping; unclipped controls)
Defoliated (clipped) plant First year of treatment during the 2007/2008 growing cycle	5 + 11 November 2007 (mid-spring; actively growing tissues) + 30 May 2008 (late autumn; dormancy)	To evaluate the cumulative effects of the first year of two defoliations on the same plant within the growing cycle on total plant production and various traits related to it (see Table 3 for measurements)
Second year of treatment during the 2008/2009 growing cycle	19 November + 20 December 2008 (late spring; actively growing tissues) + 3 June 2009 (late autumn; dormancy)	To evaluate the cumulative effects of a second year of two defoliations on the same plant within the growing cycle on total plant production and various traits related to it (see Table 3 for measurements)
Undefoliated plant First year of treatment	30 May 2008 (late autumn; dormancy)	To evaluate total plant production, and various traits related to it (see Table 3 for measurements), during the first study growing cycle
Second year of treatment	3 June 2009 (late autumn; dormancy)	To evaluate total plant production, and various traits related to it (see Table 3 for measurements), during the second study growing cycle

plant materials were dried at 70°C for 72 h and weighed.

Plant survival

At the end of autumn 2008 and 2009, number of surviving plants (SP; plants which regrow and continue growing) was counted in each of the 98 experimental plots. This allowed the calculation of percentage plant survival (PS) at a plot scale as:

$$PS = SP/IN \times 100,$$

where IN = initial plant number/plot (=12).

Statistical analyses

Our treatments were combinations of genotype \times defoliation management. Therefore, we used a factorial treatment design (7 genotypes \times 2 clipping managements) with seven replications/treatment. Data

were analysed using the statistical software INFOSTAT (Di Rienzo *et al.*, 2009). Variables that were periodically evaluated were analysed using repeated-measures two-way ANOVA. A mixed model ANOVA was used where genotype, defoliation management and genotype \times defoliation management were considered fixed effects, and sampling date, replication, and three-way interactions with sampling dates were considered random effects. The multivariate approximation was used using the statistics of Wilks (1932). Whenever an average for all sampling dates (within each of the study years) is provided for any given variable within each defoliation management and genotype, it indicates that the multivariate analysis conducted using the Wilks' statistics was not significant ($P > 0.05$). Otherwise, data are reported for each sampling date because of the interaction ($P < 0.05$) between the factors (defoliation managements, genotypes) and the sampling dates. Numbers of daughter tillers/parent tiller were transformed to $\sqrt{(x + 0.5)}$, and total dry-matter production data were transformed to

Table 3 A summary of measurements (unit) taken, and date and purpose of measurements. Results were expressed on a per unit surface area basis (i.e. per square centimetre) because of inherent differences in tiller density (tiller number per square centimetre) and plant basal area among genotypes

Measurements	Date of measurements	Purpose of measurements
Apical meristem height (cm)	2007/2008: 10 and 24 September; 8 and 22 October; 9 November 2008/2009: 9 and 23 September; 7 and 21 October; 1 and 18 November; 2 and 16 December	To determine height of the tiller apical meristem as to leave it on the plant after the defoliation managements
Plant circumference (cm)	2007/2008: 30 September; 25 October; 24 November; 27 December; 23 January; 29 February 2008/2009: 17 October; 18 November; 17 December; 22 January; 26 February	To calculate plant basal area, and thereafter express results on a per unit surface area basis (i.e. cm ²), on all study genotypes
Total (live + dry) plant tiller number	Same as for plant circumference in both years	To determine the cumulative effects of defoliation on total plant tiller number, as a measure of plant size on the study genotypes.
Number of daughter tillers/parent tiller	Same as for plant circumference in both years	To determine whether, immediately after defoliation, any of the study genotypes showed higher production of daughter tillers than the undefoliated controls as a measure of defoliation tolerance
Total tiller leaf length [blades + sheaths (green + dry); cm]	Same as for plant circumference in both years	To determine the effects of the defoliation managements on leaf growth of the study genotypes at a tiller scale
Total dry weight production (g)	2007/2008: 25 April 2008 2008/2009: 5 May 2009	To evaluate the effects of the defoliation managements on total dry weight production of the study genotypes at the end of the growing cycles, after studying some major factors (see measurements above) that determine it
Plant survival	2007/2008: 25 April 2008 2008/2009: 5 May 2009	To evaluate the effects of the defoliation managements on plant survival of the study genotypes at the end of each of the study growing cycles

In $(x + 1)$ to comply with the normality and homoscedasticity assumptions of variance (Sokal and Rohlf, 1984). Untransformed values are shown in illustrations. In all two-way ANOVA where the interaction genotype \times defoliation management was significant, both factors were analysed separately. Plant survival was analysed using two-way ANOVA. Mean separation was conducted using protected LSD, with $P \leq 0.05$. Some results were expressed on a per square centimetre basis for comparative purposes, because of plant size differences among the study genotypes. Combined analysis across the study years was not conducted because they showed similar ($P > 0.5$) monthly precipitation and temperature values during the study warm growing seasons.

Results

Height of the apical meristem

Mean height of the apical meristem at the time of the defoliation managements in 2008 and 2009 was less than or equal to 9.43 ± 0.90 mm (mean \pm 1 SE, $n = 14$) in all seven genotypes.

Green-plant basal area

Green-plant basal areas were at least 40% greater in the native (mean \pm SD: 77.1 ± 16.3 cm², $n = 22$) than in the introduced genotypes (34.0 ± 13.0 cm², $n = 90$) on average for 2007/2008 and 2008/2009. The

only exception was *E. curvula* cv. Tanganyika that showed at least a 47% greater green basal area than the other six genotypes on average for both years (data not shown). Because of differences in green-plant basal areas among genotypes, most of the traits will be presented on a per square centimetre basis for comparative purposes.

Tiller growth and demography

Tiller number per plant

Before defoliation in 2007/2008, tiller numbers of defoliated and undefoliated plants in the native species were similar ($P > 0.05$) to those in *L. cinereus* cv. 'Magnar', and *A. hymenoides* cvs. 'Paloma' and 'Rimrock' (Figure 2). A similar ($P > 0.05$) result was obtained immediately after defoliation on 24 November (data not shown). During early summer (27 December), *A. hymenoides* 'Paloma' showed a 56% greater ($P < 0.05$) tiller number than the native species and the remaining introduced genotypes. At the end of the growing season (29 February), tiller numbers of defoliated and undefoliated plants were similar ($P > 0.05$) in the native species, and in *A. hymenoides* cvs. 'Paloma' and 'Rimrock' (Figure 2). At this time, tiller numbers on defoliated and undefoliated plants of the native species were similar ($P > 0.05$) to those on undefoliated plants of *L. cinereus* cv. 'Magnar'; defoliation increased ($P < 0.05$) tiller numbers in *A. hymenoides* cv. 'Rimrock' and decreased ($P < 0.05$) them in *L. cinereus* cv. 'Trailhead' (Figure 2). Other than these cases, defoliated and undefoliated plants showed a similar ($P > 0.05$) tiller number in the native and introduced genotypes. Defoliated and undefoliated plants of *E. curvula* cv. 'Tanganyika' showed the greatest ($P < 0.05$) tiller numbers among all genotypes, but on undefoliated *A. hymenoides* cv. 'Paloma', during the full growing season. By early (23 January) and late (29 February) summer, tiller numbers were greater ($P < 0.05$) on defoliated than on undefoliated plants of *E. curvula* cv. 'Tanganyika' (Figure 2).

At the beginning of the 2008/2009 growing season (17 October), tiller numbers were similar ($P > 0.05$) in the native species and in *L. cinereus* cvs. 'Magnar' and 'Trailhead' (Figure 2). However, after the first and second defoliations towards the end of the growing season, tiller numbers were greater ($P < 0.05$) in the native genotype than in *L. cinereus* cvs. 'Magnar' and 'Trailhead', and *A. hymenoides* cv. 'Paloma' (Figure 2). From mid-spring (18 November) onwards, tiller numbers were similar ($P > 0.05$); overall mean undefoliated plants: 51.4 ± 3.0 , defoliated plants: 38.1 ± 1.6 in the native and naturalized genotypes (Figure 2). Also, from mid-spring to the end of the growing season,

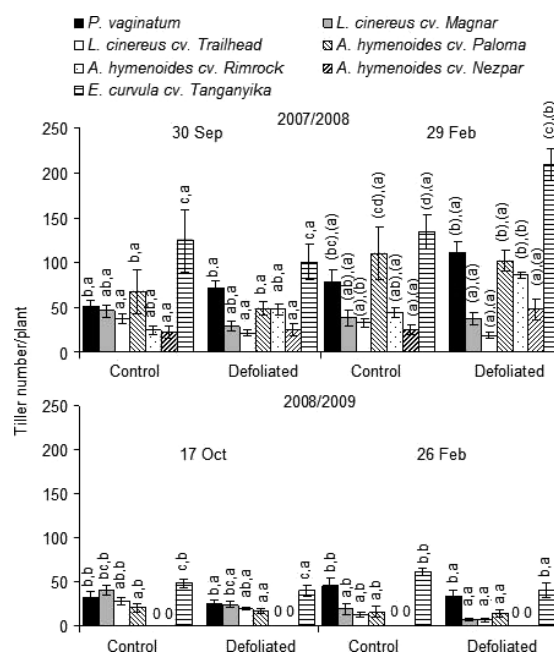


Figure 2 Tiller numbers on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. All plants were obtained from seeds. Each histogram is the mean \pm 1 SE of $n = 7$. Different letters above histograms indicate significant differences ($P < 0.05$) among genotypes (first letter) or between defoliation managements (second letter). Letters in parenthesis indicate that there was an interaction ($P < 0.05$) between genotype and defoliation management. In these cases, differences ($P < 0.05$) among genotypes within each defoliation management (first letter) and between defoliation management within each genotype (second letter) are indicated in parenthesis. Presence of zero values indicates dead plants.

defoliated plants showed at least a 12.4% lower ($P < 0.05$) tiller number than the undefoliated controls in the native and naturalized genotypes, and in *L. cinereus* cvs. 'Magnar' and 'Trailhead', and *A. hymenoides* cv. 'Paloma' (Figure 2).

Tiller number per plant across all genotypes increased by more than 19% on undefoliated and 88% on defoliated plants from early spring to late summer in 2007/2008 (Figure 2). However, during early spring and late summer of the next year, tiller number per plant across all genotypes had decreased at least 54% on defoliated and undefoliated plants (Figure 2).

Tiller number per square centimetre

Defoliation management and genotype interacted with time in 2007/2008 and 2008/2009. This is because

data were analysed within each date. During most of the sampling dates during the first and second years, defoliated and undefoliated plants showed a similar ($P > 0.05$) tiller number per square centimetre (30 September: 1.46 ± 0.18 , 25 October: 1.45 ± 0.15 and 24 November 2007: 1.38 ± 0.15 ; 29 February: 1.85 ± 0.19 , 17 October: 0.50 ± 0.08 , 18 November: 0.52 ± 0.10 , and 17 December 2008: 0.53 ± 0.11 ; 22 January: 0.47 ± 0.11 , and 26 February 2009: 0.35 ± 0.10). The only exceptions were on 27 December 2007 and 23 January 2008, when tiller number per square centimetre was lower ($P < 0.05$) on undefoliated (2007: 1.43 ± 0.24 ; 2008: 1.71 ± 0.30) than on defoliated (2007: 1.88 ± 0.21 ; 2008: 2.35 ± 0.30) plants.

During the first and second years, tiller number per square centimetre was similar ($P > 0.05$) between the native and naturalized genotypes (Figure 3). In both years, this variable was similar ($P > 0.05$) or greater ($P < 0.05$), but not lower, in the introduced than in the native or naturalized genotype (Figure 3). Plants of *A. hymenoides* cvs. 'Rimrock' and 'Nezpar', however, were dead by the initiation of the second year.

The reduction in tiller number per square centimetre across all genotypes between the first and second years was $>78\%$ (Figure 3).

Daughter-tiller production per unit surface area

Defoliated and undefoliated plants of *A. hymenoides* cvs. 'Paloma' and 'Rimrock' showed a greater ($P < 0.05$) daughter-tiller production than the native and the remaining genotypes in 2007/2008 (Figure 4). In this year, production of daughter tillers by the native species was similar ($P > 0.05$) to that of *L. cinereus* cv. 'Trailhead', *A. hymenoides* cv. 'Nezpar' and *E. curvula* cv. 'Tanganyika' and greater ($P < 0.05$) than that of *L. cinereus* cv. 'Magnar' (Figure 4). During the following growing season (2008/2009), however, the greatest ($P < 0.05$) daughter-tiller production was determined in the native genotype, and production of daughter tillers was similar ($P > 0.05$) in the remaining six genotypes (Figure 4). In 2007/2008 and 2008/2009, daughter-tiller production was similar ($P > 0.05$) on defoliated vs undefoliated plants in all genotypes (Figure 4).

Between the first and second years, the reduction in the production of daughter tillers across all, but the native, genotypes was $>90\%$ on defoliated or undefoliated plants (Figure 4). The only exception was the defoliated and undefoliated plants of *P. vaginatum*, which maintained an overall daughter-tiller production of 0.0100 ± 0.0004 tillers per square centimetre between both years (Figure 4).

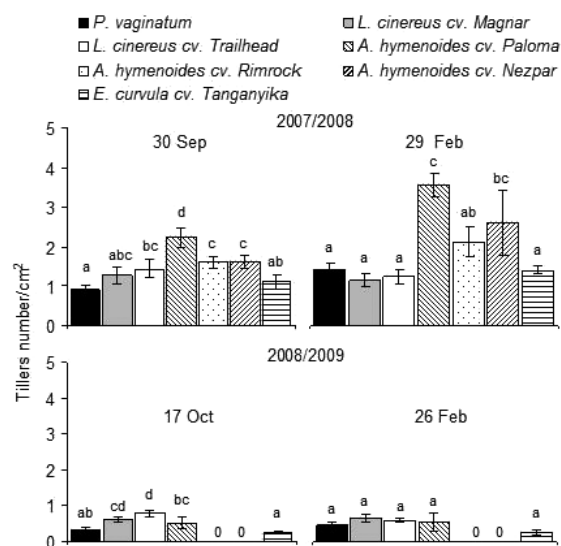


Figure 3 Tiller numbers per square centimetre of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. All plants were obtained from seeds. Data for Control and Defoliated plants were pooled after there were no significant differences ($P > 0.05$) among them. Each histogram is the mean \pm 1 SE of $n = 14$. Within each date, different letters above histograms indicate significant differences ($P < 0.05$) among genotypes. Presence of zero values indicates dead plants.

Total leaf length

Before defoliation in 2007/2008, total leaf length per unit surface area was similar ($P > 0.05$) (i) among genotypes and (ii) between defoliated and control plants (Figure 5). The only exception was *A. hymenoides* cv. 'Nezpar' that showed greater ($P < 0.05$) total leaf length than that in the other genotypes (Figure 5). After the two defoliations events in 2007, defoliated and undefoliated plants of (i) *Leymus cinereus* cv. 'Trailhead', and *A. hymenoides* cvs. 'Rimrock' and 'Nezpar' on 24 November 2007; (ii) *A. hymenoides* cv. 'Nezpar' on 27 December 2007; (3) *L. cinereus* cvs. 'Magnar' and 'Trailhead', and *A. hymenoides* cvs. 'Paloma' and 'Nezpar' on 23 January 2008, and (iv) *L. cinereus* cvs. 'Magnar' and 'Trailhead' and *A. hymenoides* cv. 'Nezpar' on 29 February 2008 showed at least 150% greater ($P < 0.05$) total leaf lengths than those on the native species (Figure 5).

After defoliation, total leaf length was at least 15% lower ($P < 0.05$) on defoliated than on undefoliated plants in all genotypes from 24 November 2007 to 29 February 2008 (Figure 5). The only exception was on *L. cinereus* cv. 'Magnar' where total leaf length was

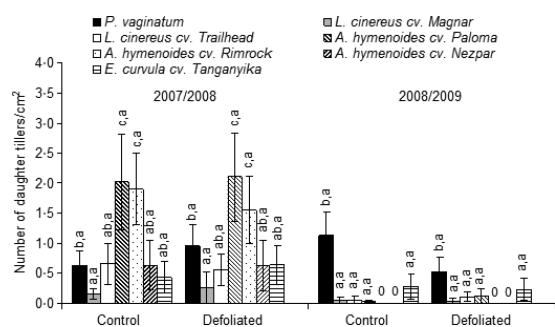


Figure 4 Number of daughter tillers per square centimetre on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. Each histogram is the mean \pm 1 SE of $n = 42$ (2007/2008) or $n = 35$ (2008/2009). Within each growing cycle, different letters above histograms indicate significant differences ($P < 0.05$) among genotypes (first letter) or between defoliation managements (second letter). Presence of zero values indicates dead plants.

similar ($P > 0.05$) on defoliated than on undefoliated plants on 29 February 2008 (Figure 5).

In the next growing cycle (2008/2009), defoliated and undefoliated plants of (i) *L. cinereus* cvs. 'Magnar' and 'Trailhead' and *A. hymenoides* cv. 'Paloma' on 17 October and (ii) *L. cinereus* cvs. 'Magnar' and 'Trailhead' on 18 November showed greater ($P < 0.05$) total leaf length than the native species (Figure 5). On 17 October and 18 November 2008/2009, defoliated and undefoliated plants showed similar ($P > 0.05$) total leaf lengths in all genotypes (Figure 5). From 17 December 2008 to 26 February 2009, total leaf length was on average more than 70% greater ($P < 0.05$) in *L. cinereus* cv. 'Trailhead' than in the native genotype, *L. cinereus* cv. 'Magnar', *A. hymenoides* cv. 'Paloma' and *E. curvula* cv. 'Tanganyika' (data not shown). Once again, defoliated and undefoliated plants showed a similar ($P > 0.05$) total leaf length in *P. vaginatum*, *L. cinereus* cvs. 'Magnar' and 'Trailhead', *A. hymenoides* cv. 'Paloma' and *E. curvula* cv. 'Tanganyika' (data not shown).

In early spring, the total leaf-length reduction across all genotypes from 2007 to 2008 was 80.9% on control plants and 78.3% on defoliated plants (Figure 5). By late summer, the reduction in total leaf length across all genotypes between the first and second years was more than 66% on defoliated and undefoliated plants (data not shown).

Total dry-weight production

No significant differences ($P > 0.05$) in production of total dry weight were found among genotypes during

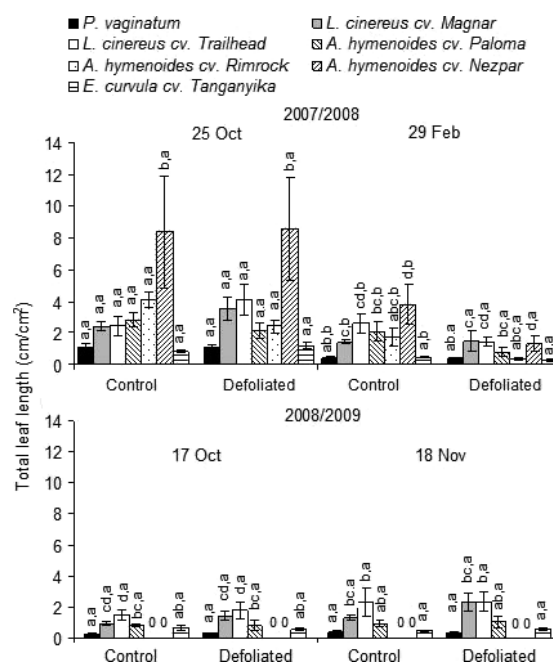


Figure 5 Total leaf length [length of total blades + sheaths (green + dry)/cm²; cm/cm²] on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated) during the growing seasons of 2007/2008 and 2008/2009. Each histogram is the mean \pm 1 SE of $n = 7$. Within each growing cycle, different letters above histograms indicate significant differences ($P < 0.05$) among genotypes (first letter) or between defoliation managements (second letter). Presence of zero values indicates dead plants.

2007/2008 (Figure 6). At the same time, however, total dry-weight production was greater ($P < 0.05$) on defoliated than on undefoliated plants of all genotypes (Figure 6). During 2008/2009, *L. cinereus* cv. 'Magnar' showed a greater ($P < 0.05$) total dry-weight production than the native genotype, while production of total dry weight was similar ($P > 0.05$) in *P. vaginatum*, in *L. cinereus* cv. 'Trailhead', *A. hymenoides* cv. 'Paloma' and *E. curvula* cv. 'Tanganyika' (Figure 6). Total dry-weight production was similar ($P > 0.05$) on defoliated versus undefoliated plants in all study genotypes in 2008/2009 (Figure 6).

There was a substantial reduction in total dry-weight production across the genotypes on defoliated (76.1%) and undefoliated (59.7%) plants between the first and second years (Figure 6).

Plant Survival

Greatest ($P < 0.05$) percentage survival at the end of the 2007/2008 growing season was found on defoliated

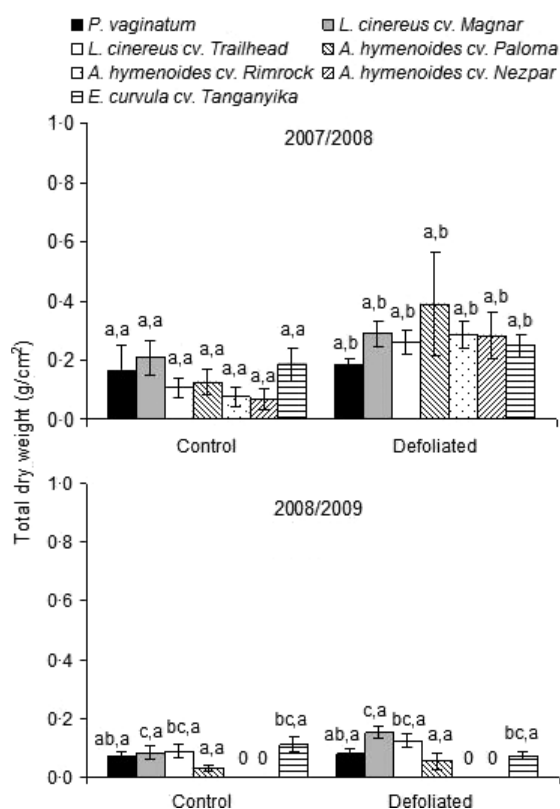


Figure 6 Total dry-weight production per square centimetre in 2007/2008 or 2008/2009 on plants of seven (2007/2008) or five genotypes (2008/2009) exposed to two defoliation managements (Control, Defoliated). Each histogram is the mean \pm 1 SE of $n = 7$. Within each growing cycle, different letters above histograms indicate significant differences ($P < 0.05$) among genotypes (first letter) or between defoliation managements (second letter). Presence of zero values indicates dead plants.

and undefoliated plants of the native (mean = 83.3%) and naturalized (mean = 74.4%) genotypes (Figure 7). These values approximately double those found in the introduced genotypes (overall mean = 36.9%), but *A. hymenoides* cv. 'Nezpar' presented the lowest ($P < 0.05$) plant survival (Figure 7). During the second growing season (2008/2009), defoliated and undefoliated plants of the native species showed the greatest ($P < 0.05$) plant survival (mean = 71.4%, Figure 7). Percentage survival was on average 35% lower ($P < 0.05$) in the naturalized genotypes that presented greater ($P < 0.05$) values than on those introduced (Figure 7). Defoliated and undefoliated plants of *A. hymenoides* cvs. 'Nezpar' and 'Rimrock' were dead at the end of the 2008/2009 growing cycle (Figure 7). Plant survival was greater on undefoliated than defoliated

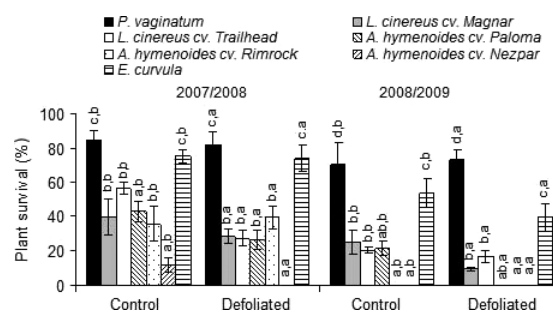


Figure 7 Percentage survival of seven genotypes exposed to two defoliation managements (Control, Defoliated) at the end of the growing seasons of 2007/2008 or 2008/2009. Each histogram is the mean \pm 1 SE of $n = 7$. Absence of histograms indicates zero values (i.e. dead plants). Within each growing cycle, different letters above histograms indicate significant differences ($P < 0.05$) among genotypes (first letter) or between defoliation managements (second letter).

plants across all genotypes during both growing seasons (Figure 7).

Discussion

At least during the first 3 years of growth and development in these species, height of the growth apex was below 1 cm from the soil surface during spring in the north-western region of arid Patagonia, Argentina. This finding is important because livestock could graze *L. cinereus* genotypes during spring without removing most active intercalary and apical meristems, at least during the first 2 years after plant establishment. This means that growth will continue to be rapid after spring grazing, because growth rate is fastest from intercalary meristems, intermediate from the leaf primordial in the growth apex and lowest from the activation and subsequent outgrowth of the axillary buds (Briske and Richards, 1995). As active meristems remained on the plant after the defoliation events, they might be able to recuperate their tissues lost to defoliation. However, the fact that active meristems measured in this study were at 1 cm did not guarantee persistence of *L. cinereus* in our study. This was the result of the fact that *Leymus* genotypes defoliated at 5 cm, in a spaced plant situation, lost 60% of the plants in the first season and more than 80% in the second. Other studies in the western rangelands of the USA have reported that this genotype needs to be clipped to no less than 30 cm height for reducing grazing damage (USDA, NRCS, 2000).

Plants of *Eragrostis curvula* cv. 'Tanganyika' showed the greatest basal area during the first and second years and the greatest tiller number per plant during

the first growing season among all genotypes. Fernández *et al.* (1991) reported that vegetative tillers in *E. curvula* cv. 'Tanganyika' multiply rapidly during the growing season, that is, hundreds of them can be originated on a plant basis during the plant establishment year under favourable biotic and abiotic conditions. During the first year, defoliation increased tillering in *E. curvula*. Tillers at the periphery are often exposed to a greater radiation intensity than those at the plant centre, where shading might be high (Briske and Richards, 1995). Defoliation might have reduced shading and increased the quantity and quality of light reaching the crown at the plant centre. The positive effects of defoliation on tillering of *E. curvula* were only shown during the first year. During the second year, tiller numbers per plant in December on plants of all genotypes and those of *E. curvula* were similar to those in the native species from before the first defoliation to the end of the growing season.

The cumulative effects of two successive years of severe defoliations reduced tiller number on plants of all genotypes. These adverse effects of defoliation on tillering of perennial grasses have been reported by various authors (Briske and Richards, 1995). Defoliation has caused (i) inhibitory effects on activation and viability of axillary buds (Busso *et al.*, 1989); (ii) a reduction in carbon reserve availability that allows initial re-growth when a photosynthetic surface area is not available after a disturbance (Busso *et al.*, 1990); and (iii) a lower survival of growing tillers (Busso *et al.*, 1989).

Plants of the native species showed a greater basal area and had a similar or lower tiller number than those of the introduced genotypes, especially with respect to *L. cinereus*, after the first-year defoliations. At this time (i.e. end of the first growing season), tiller number on defoliated plants was similar to or greater than, but not lower than, that on undefoliated controls in all genotypes (but *L. cinereus* cv. 'Trailhead'), which is an indication of defoliation tolerance. *Pappophorum vaginatum* was affected by defoliation during the second study year, which produced a reduction in the basal area of their plants. The only genotype that showed an equal or greater tiller number per plant than *P. vaginatum* in the first growing season was *A. hymenoides* cv. 'Paloma'. This introduced species was unable to have a greater basal area, but its tillers were thinner (Torres, 2010) than those in the native genotype.

At the beginning of the growing season, regrowth from axillary meristems was about 3 weeks earlier in *L. cinereus* cv. 'Magnar' than in *P. vaginatum*. This response in cv. 'Magnar' would contribute to an earlier occupancy of the more favourable soil parcels, which in turn should improve competitive effective-

ness. Favourable soil microsites may be important areas of root competition (e.g. Jackson and Caldwell, 1989). This could help explain the earlier shoot re-growth in early spring in *L. cinereus* than in *P. vaginatum*. The fact that the C₃ genotype started growth earlier than the C₄ one agrees with the report of Niu *et al.* (2008). These authors stated that the C₃ species begin growth in early spring, soon after the soil temperature is above freezing, while C₄ species grow during warmer periods.

In the two study growing seasons, total leaf length was most often greater in the introduced *Achanatherum* or *Leymus* species than in the native genotype. Moreover, total leaf length in 2007/2008 was greater on defoliated than on undefoliated plants of *L. cinereus* cv. 'Magnar', thus showing tolerance to defoliation. At the end of the 2008/2009 growing season, total leaf length produced between the second defoliation in 2008, and the end of the experiment, was similar on defoliated than on undefoliated plants in all study genotypes. This indicates that leaves grew faster on defoliated than on undefoliated plants after defoliation to reach equal total leaf lengths at the end of the growing season.

Except for *L. cinereus* cv. 'Magnar', where daughter-tiller production was greater in the native than in the introduced genotype, daughter-tiller production was similar or greater in the introduced genotypes than in the native species in the first growing season (2007/2008: 222.5 mm from September 2007 to May 2008; 123 mm from September to November 2007). The dry 2008/2009 growing season (September 2008 to May 2009: 131.5 mm; 29.5 mm from September to November 2008) might have contributed to determine a lower daughter-tiller production in the introduced and naturalized than in the native genotype. In both years, daughter-tiller production was similar on defoliated than on undefoliated plants in all genotypes. This means that defoliation did not hinder daughter-tiller production, which we know contributes to defoliation tolerance (Briske and Richards, 1995), even under dry conditions.

The serious reduction in tiller numbers, especially daughter-tiller numbers, on defoliated and undefoliated plants across all genotypes from the first to the second year might be in part the result of the dry growing season in 2008/2009. Tiller number is an indication of bud outgrowth (Busso *et al.*, 1989). These authors emphasized that defoliated tillers on drought-treated plants of the bunchgrass *Pseudoroegneria spicata* (Syn: *Agropyron spicatum*) showed a significantly lower number of physiologically active buds than tillers on undefoliated controls in that treatment. Flemmer *et al.* (2002) also determined in various perennial grasses that the proportion of stem bases producing tillers per

plant was much lower under water stress than under higher levels of soil-moisture availability. Additionally, crown and total (crown + roots) pools of total non-structural carbohydrates were positively associated with early spring tiller regrowth on two perennial bunchgrass species (Busso *et al.*, 1990). Therefore, we suggest that the great reduction in tiller numbers from one year to the next in our study could be a sign of a depleted plant in both axillary bud bank and energy reserves. These two factors might have contributed to the high plant mortality at the end of the study in the introduced genotypes. Additionally, Hodgkinson (2010) reported that the density of live tillers generally declined on plants of the perennial grasses *Ausrodonthia auriculata*, *Bothriochloa macra*, *E. curvula*, *Phalaris aquatica* and *Themeda triandra* as they remained under drought conditions. Furthermore, he showed that the death of plants in the drought treatment began for all species very soon after the foliage of plants had died. Hodgkinson (2010) determined a critical threshold for days in drought beyond which all plants of any of his study species would die, which was species dependent: about 100 days for *A. auriculata*, *P. aquatica* and *T. triandra*, 200 days for *B. macra* and 300 days for *E. curvula*.

After the second defoliation in 2007/2008, by mid-spring, growth rates (on a total leaf-length basis) were between 0.009 ± 0.001 and 0.205 ± 0.081 cm cm⁻² d⁻¹ on defoliated and 0 cm cm⁻² d⁻¹ on undefoliated plants of all genotypes. Rapid leaf replacement after defoliation is a critical component of defoliation tolerance in various perennial grass species (Briske and Richards, 1995). The number of active meristems and the amount of residual photosynthetic surface area have been reported to be more important than carbon reserves in limiting regrowth rates on defoliated plants (Richards and Caldwell, 1985). Also, changes in environmental conditions, especially at the level of apical meristems, have fostered leaf growth on defoliated plants (Briske and Richards, 1995). Rapid leaf replacement after defoliation in other grasses has been attributed to compensatory photosynthesis on leaf and stem tissues, increases in tissue longevity or increases in the water status of defoliated plants (Briske and Richards, 1995). Leaf replacement was rapid immediately after defoliation. However, it was not great enough as to allow leaf lengths to be either similar or greater on defoliated than on undefoliated plants in all genotypes during the first year (but in *L. cinereus* cv. 'Magnar').

Leaf lengths per unit basal area between both defoliation managements in all genotypes were similar immediately after defoliation in 2008/2009. Water stress conditions at this time (during November and December, when defoliation occurred, rainfall was 0.5 and 32.5 mm respectively, and potential evapotranspi-

ration was 139.8 and 155.4 mm respectively) very likely constrained defoliated plants from growing faster than the undefoliated controls. The effect of water stress in constraining growth of defoliated plants has been observed in various perennial grasses (Busso *et al.*, 1989, 2003).

Dry-matter production was similar in the native than in most of the introduced genotypes during both study years. During the second growing season, dry-matter production was similar in the native and naturalized species, but greater in *L. cinereus* cv. 'Magnar' than in the native species. Defoliated plants of all genotypes showed a greater dry-matter production than the undefoliated ones during the first study year. This is an indication that defoliated plants tolerated defoliation. However, the dry 2008/2009 may have constrained defoliated plants from reaching a greater dry-matter production than their undefoliated counterparts. Mohammad *et al.* (1982) found that the amount of regrowth in *Agropyron desertorum* and *Elymus junceus* was inversely related to the increased water stress to which plants had been previously exposed. The low rainfall (29.5 mm, Figure 1) during the most active growth period (early to mid-spring: September to November) in 2008/2009 and the cumulative effects of two successive years of two severe defoliations annually (which determined substantial reductions in tiller numbers per plant, production of daughter tillers per square centimetre, total leaf length per square centimetre and plant survival) contributed to reductions in plant dry weight per square centimetre between the first and second years. The negative effects on plant growth of the combined influence of water stress periods and at least one severe defoliation during two or more consecutive years have been demonstrated in various perennial grass species from temperate regions (Busso *et al.*, 1989, 2003). Like in our study, these research works indicated that the difference in plant responses between consecutive years can have great biological significance.

We have to highlight that the drier 2008/2009 than 2007/2008 conditioned plant responses to defoliation and increased difficulty in interpretation of results. It is well known that plant growth and survival, and tiller formation are very sensitive to water stress (Busso *et al.*, 1989; Briske and Richards, 1995). The native and naturalized species and *L. cinereus* showed better performance than the remaining genotypes after defoliation under water stress in the growing season of 2008/2009. Blades of *L. cinereus* cv. 'Trailhead' which grew at the study site, for example, showed osmotic adjustment (Torres *et al.*, 2010). This physiological mechanism allows plants to sustain leaf growth under severe water-stress conditions (Kirkham, 2005). *Achanatherum hymenoides* cvs. 'Nezpar'

and 'Rimrock' showed an important leaf production (Torres, 2010), but they did not survive beyond the first study year.

Plant survival was greater in the native species than in the introduced genotypes. Similar results have been reported for other species in *Pappophorum* under grazing conditions (Privitello *et al.*, 1998). Survival values shown by *L. cinereus* and *A. hymenoides* after 2 years of study were lower than those reported by other authors on different environmental conditions and defoliation managements (Tilley, 2005). However, several authors reported difficulties for plant establishment of *L. cinereus* and *A. hymenoides* in various semi-arid regions of the USA (Vogel and Jensen, 2001). In this study, plants were grown from seeds at the greenhouse, and seedlings were transplanted to plots on single rows of space-transplanted plants on 1.1 m centres. Fernández *et al.* (1991) reported that failure of *E. curvula* introduction in the study region is due to its reduced seed size and low growth rates when precipitations are low.

Climate on semi-arid and arid areas has a great influence on plant populations not only because precipitation is low but also because its distribution during the growing season is unpredictable (Huxman *et al.*, 2004). Plant establishment is often related to high precipitations during certain times, while plant mortality is correlated with extended low precipitation periods (Turner, 1990). Bleak *et al.* (1966) and Roundy (1985) have emphasized the high sensitivity of plant establishment to water stress of *L. cinereus* and *A. hymenoides* in areas receiving less than 200 mm annually. In 2008/2009, precipitations were 29.5 mm from September to November (the most active growing period), 92 mm from December to February and 10 mm from March to May.

We have to acknowledge a limitation in this study: the introduced genotypes are intended for grazing, but they were assessed under clipping. It is well known that clipping at a given height does not adequately mimic grazing. The primary reasons for this difference are that (i) grazing does not remove uniform amounts of forage from all tillers, hence tiller removal from plants is unrealistically severe, and (ii) grazing animals have substantial indirect effects such as soil compaction and recycling of nutrients via dung and urine (Asner *et al.*, 2004). The greater production or growth on grazed than clipped plants has been partially attributed to the non-uniform nature of herbivory (Parsons *et al.*, 1984).

We have to reject our hypothesis because daughter-tiller production and the subsequent dry-matter production were most often similar or greater on the introduced than on the native genotype during the two study years. Plant survival at the end of the study, however, was greater in the native than in

the introduced genotypes. Plant of these introduced genotypes showed a weakened stage into the second, dry year, leading to reduced growth variables, and a high plant mortality at the end of the study. As a result, further studies should focus on improving plant persistence of the introduced genotypes. There is a worldwide need for developing more appropriate forage resources for arid and semi-arid grasslands and rangelands (Torres, 2010).

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